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FURTHER STUDY OF AN ANT.

BY ADELE M. FIELDE.

Argument.—That *Stenamma fulvum piceum*¹ is the bearer of three distinct odors, perceived through the three distal segments of her antennæ: (*a*) A scent deposited by her feet, forming an individual trail, whereby she traces her own steps, discerned through her tenth segment; (*b*) an inherent and inherited odor, manifested over her whole body, identical in quality for queens and workers of the same lineage, a means for the recognition of blood-relations, discerned by contact of the eleventh segment; (*c*) a nest-smell, consisting of the commingled odors of all animate members of the colony, diffused by them in air or ether, constituting an aura whereby they distinguish their nest from those of aliens and discerned through the twelfth, the distal, segment.

That her behavior is influenced by a sensory memory; and that while, without experience or instruction, she capably constructs the dwellings of her species and tends the young, her criterion of a nest-aura is established solely by association, and may be changed many times during her life.

That her care of the young is a reflex from the eighth and ninth segments of her antennæ; and that she receives an immediate reward for her labor in the sustenance thereby obtained.

That the gregarious habit of the ant is a conjoint result of the reflexes from the five distal segments of her antennæ.

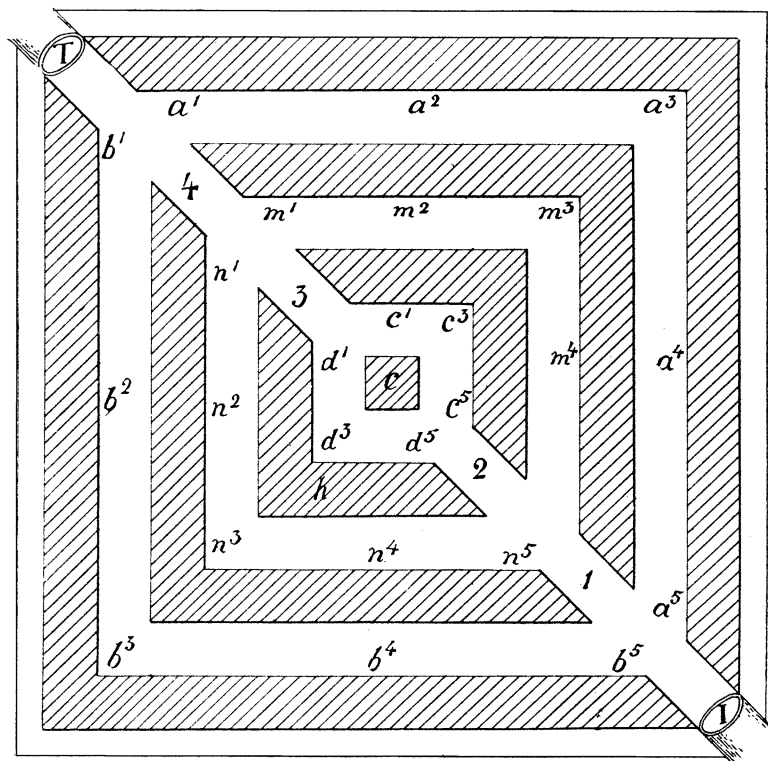
An Oriental folk-story ascribes to the ant a keen sense of smell,² and Occidental biologists grant its possession of this faculty.

I have recently carried on experiments,³ using the maze herein described, whereby I believe it to be shown that *Stenamma fulvum piceum*, aided by a sensory memory, finds her way by means of an individual scent deposited from her feet, and that her perception of this scent is through the tenth segments of her antennæ.

¹ *Stenamma (Aphaenogaster) fulvum*, Mayr; subspecies *aquila*, Buckley; variety *piceum*, Emery.

² "The Origin of Ants," in *Chinese Nights' Entertainment*, by A. M. Fielde: G. P. Putnam's Sons, 1894.

³ At the Marine Biological Laboratory, Woods Hole, Mass., May to October, 1901.



THE MAZE.

The floor of the maze was a pane of clear glass laid upon white cardboard, upon which the runs were indicated by letters and figures. The runs were twelve millimeters or a half inch wide, and were separated by walls twelve millimeters high and twelve millimeters thick, built of strips of glass closely joined to one another and to the floor by LePage's liquid glue, and dried during several months before the maze was used in experiment. The walls were topped by a layer of cotton wadding which was removed and renewed whenever the maze was cleaned for a new experiment. The roof, laid upon the wadding and closing the maze at the top, was a square of thin clear glass diagonally divided across a^3-b^3 , for convenience in uncovering only half the maze at a time. Effort was made to secure the same degree of light, warmth and humidity in every part of the maze.

At I a straight glass tube seven centimeters long communicated with a small nest in which the ant household used in the experiment had been long established. The tube I , as well as the nest, was completely darkened, and was opposite the source of light.

At T a glass tube, bent upward at its outer end, gave ingress to the ants from my hand and was stopped by a plug of cotton when not in use.

The distance from T to I was twenty-one centimeters, a little more than eight inches.

I placed some hundreds of pupæ at the *T* corner, and taking marked and unmarked ants from the nest *I*, introduced them to the maze through the tube, *T*. In no case, except when manifestly lost, did any ant carry⁴ in a pupa without having first made the journey without a burden. Sometimes an ant traversed more than one run before she began the labor of carrying in, and if she afterward used more than one of the runs she never used other than those she had previously traversed, no matter how many of her fellow burden-bearers were travelling the other routes. If the glass floor was clean she apparently had greater difficulty in establishing her trail than when the floor was covered by wood or by earth. In the first case, she would go a short distance, as from *T* to a^2 or n^2 , and return, and then would prolong her next journey as far as a^3 or n^3 , and she might make many excursions from *T* over the same path before she discovered the entrance to the nest at *I*. When the floor was covered with earth a single trip often sufficed, and she began to carry in when on her second excursion from *T*. The structure of the ant's feet adapts them to the partial clasping of particles of earth, and it may be that pressure assists in the deposit of the scent.

Having begun to carry in, an ant usually continued her work incessantly, making from thirty-seven to seventy round journeys in an hour. No burden-bearing ant ever made a loop in her own trail. The shortest run, *c-d*, was not oftenest taken, but no ant ever carried in by a route longer than a single run, *a*, *m*, *c-d*, *n* or *b*.

The *c-d* run virtually counted as but one, for when any ant had made the *c* or the *d* passage, she afterward used either side of the central block *c* with little hesitation.

There was no evidence that any ant was influenced by the fact that the *c-d* run was shortest, and that there were certain advantages in following a straight line; but we should not therefore hastily declare that ants have no reasoning power. The Chinese, for reasons well known to themselves, generally make their roads crooked.

The ingoings and returns of several marked ants during one

⁴The ants withdraw their young from currents of air even more quickly than from light. If the ants huddled upon the pupæ, making their own bodies a screen from the light, they were impelled by my gently blowing into the tube *T* to search for a tranquil refuge in the nest.

hour were recorded. *Dot One* made seventy-two journeys, going in and returning by the *c-d* run. Deviations, apparently caused by pressure or by momentum, were sometimes made on departing from *T* or from *I*, but she never deviated from her trail more than four times her own length without discovering her error and retracing her path into the *c-d* run.

Dot Two made sixty-one round journeys by the *c-d* run. Other ants were at the same time going in and returning by the same and by other routes.

Dot Three made forty round trips. The first fourteen were all by the *n* run. She was then carried, apparently by her own momentum under a heavy burden, into the *a* run, and there wandered to and fro, utterly lost, notwithstanding the frequent passing of her comrades. She eventually made her way by the *a* run into *I*. Somewhat later, under similar momentum, she likewise floundered through *c-d*, and then at intervals she afterward, with no hesitation, four times took the *c-d* route to *I*. All her other ingoings and all her returns were via the *n* run. A few hours later, when I again set the ants to work, *Dot Three* again took the *n* route, and in an hour made forty-eight round trips thereby. A few times she made impetuous starts into other runs, but she every time retraced her steps and followed her best-known path. I then removed her to a Petri cell, closed the entrances to all runs other than *c-d* and *m*, and put several unmarked ants to the work of carrying in pupæ. During that afternoon and the succeeding forenoon, these ants made over three hundred round trips through *m* and *c-d*. When these two runs had thus been thoroughly scented by other ants, and while their trails were yet fresh, I unclosed all the runs and put *Dot Three* in through *T*. After an absence of nineteen hours, she made her first trip, without a burden, through *n*, and then resumed the carrying in of pupæ, making fifty-four round journeys in an hour, going in forty-eight times by the *n* run and six times by the *c-d* run, and returning fifty-two times by the *n* run and twice by the *c-d* run. Not once did she enter the *m* run, which had during the previous hour been traversed hundreds of times by her comrades.

The following day, no use having been made of the maze in the interval, I again put *Dot Three* in at *T*. She at once went, without a burden, through *a*, and returned through *n*. During the

next hour she made forty-six burden-bearing journeys through n , returning forty-five times through n and once through c . She undertook to carry in a larva larger than herself and, after protracted and ineffective effort, dropped it at n^4 , returned, and then carried in a very small larva. On subsequent journeys she repeatedly passed over or close beside the dropped larva, but she seemed to be aware that it had proven too heavy for her, and did not renew her attempt to lift it.

I then, during her absence in the nest, removed the earth over a space of one centimeter from the floor at n^2 , and washed the glass floor and the neighboring walls and roof. On her return she crossed the space unhesitatingly to the pupæ pile at T , made two burden-bearing journeys, one *via* c , one *via* a , with both returns *via* n . She then came and examined the cleaned space, burrowed in the bank at its sides, went to and fro several times over it, and resumed her carrying in through this n run.

Dot Four having first made without a burden excursions through the b , c , n , and a runs, made fifty-five consecutive burden-bearing journeys, going in forty-five times by the a , twice by the m , four times by the $c-d$, and four times by the n run. Her returns were forty-nine times by the a , once by the m , twice by the c , and three times by the n run. The b run was not again entered. I then isolated her in a Petri cell, and two days later, having stopped the a run with plugs of cotton, I returned her to the maze through T . She at once tried to enter a , pushing at the cotton and endeavoring to creep under or over it. Finding it impassible, she made several journeys through m . I then isolated her two days more, unstopped a , and returned her to the maze through T . She resumed her route through m , and made six round trips by that run which she had used while a was stopped, then she made a return through a , her older path, and from that time all her ingoing journeys and returns were made by that route.

Dot Five made sixty round trips, of which twenty-eight ingoing journeys were made by the m , thirty-one by the a , and two by the $c-d$ run. Of her returns fifty-two were made by $c-d$ and nine, at intervals, by m . When she had passed thirty-seven times through m , I laid across its floor, at m^2 , while she was at T , a strip of paper one centimeter wide. As soon as she reached it she turned back with her burden and went in by $c-d$, returning as

usual by $c-d$. Twice more she likewise came to the paper, and although several other ants had meantime passed over it, she retraced her steps into $c-d$, and thereafter made no more excursions into m , going always through $c-d$.

Dot Six entered the maze at T , made her first round trip, without a burden, through m , then took a false start into $c-d$, wandered there, reached $\mathcal{Q}$, returned to m^1 and followed the m run to the nest. Thereafter she made nineteen journeys, going in fifteen times through m and four times through n , and returning once through n , and eighteen times through $c-d$. I then put a barrier across $\mathcal{Q}$, expecting her to turn back and take the m or n route, but in returning on her trail she discovered what neither the ants nor I had before observed, a small hole in the glass wall at h , and through this hole she reached n . After that her journeys, made with no hesitation, were as follows:

INGOING.		RETURNING.	
1	via n	1	via n
2	" $d-h-n$	2	" "
3	" "	3	" "
4	" n	4	" "
5	" "	5	" "
6	" $d-h-n$	6	" "
7	" "	7	" $n-h-d$
8	" n	8	" "
9	" $d-h-n$	9	" "
10	" n	10	" "
11	" $d-h-n$	11	" "
12	" n	12	" "
13	" $d-h-n$	13	" n
14	" n	14	" "
15	" "	15	" $n-h-d$
16	" $d-h-n$	16	" "
17	" "	17	" "
18	" "	18	" "
19	" "	19	" "
20	" n	20	" "
21	" "	21	" "
22	" $d-h-n$	22	" n
23	" "	23	" "
24	" "	24	" "
25	" "	25	" $n-h-d$

After *Dot Six* had several tens of times passed through the hole in the wall, I stopped the runs from $c-d$ at $\mathcal{Q}$ and at $\mathcal{S}$, enclosing two burden-bearing ants and a dropped pupa. The two ants had trails directly to I , and when they found themselves unable to proceed through $\mathcal{Q}$ they turned back and repeatedly explored all

parts of *c-d*. It was plain that the trail of *Dot Six* through the hole gave them no guidance. At last one of the two ants found the hole, passed through it, made her way in, returned and carried in the dropped pupa, passing the hole the second and third times with no hesitancy. The trail of this ant, added to that of *Dot Six*, apparently gave no clue to the remaining ant, for she continued to hunt for an exit until she, too, finally found the hole for herself, and went through it to I. During succeeding hours, after 2 and 3 were unstopped, no more than the three ants, including *Dot Six*, ever used the hole as a passageway.

While the ants were carrying in pupæ, one of the two queens in the nest twice came out to the *T* corner, examined the pupæ pile and went back, but no worker changed her route to follow that of the queen.

It is evident from the foregoing records, giving examples taken from among many made, that the ant followed her own trail, taking it in either direction with equal facility. She was doubtless influenced in her course by the topography of the ground. *Dot Seven* always went in through the *b* run, passing close to the outer wall at *b*⁵. On returning she usually mounted a corner of the inner wall near *b*⁵ and scrambled down its vertical face. The latter route was feasible for a return journey, but impracticable for her when she carried a burden.

When the ants regularly took one route for the outgoing and another for the ingoing trip, they appeared to follow the line of least resistance, or to be influenced by convenience. I have repeatedly seen ants change their customary route when they found their progress hindered by other ants that were taking the same or the opposite course. When ants journey in numbers they go by one route and return by another, as human throngs divide, for mutual advantage, into two processions for crossing a bridge, one moving to the right, the other to the left.

The ants cannot follow the trail of a foe. An intruder whose aura has alarmed the colony may pass close to a resident, alert on the warpath, and the resident will run to and fro with no clue to the exact location of the enemy until the touch of an antenna reveals it.

Bethe holds that there is a polarization of the scent,⁵ showing

⁵ Albrecht Bethe, *Dürfen wir den Ameisen und Bienen physische Qualitäten zuschreiben*. Pflüger's Archiv, Vol. 70, Jan., 1898.

the ant the direction toward or away from the nest. He caused ants to make a path across a board, a section of which could be made to revolve 180° . When the section was reversed, an ant reaching the section from either direction was unable to directly proceed. If the section was not reversed until the ant was upon it, the ant would continue its way across the section, but on coming to the end of the section would stop and give evidence of having lost its trail.

Perhaps by reversing the section the continuity of the individual trail was broken, the ant being therefore unable to directly proceed. My experiments show that the theory of polarization of the scent is untenable. *Dot Five*, after establishing her trail, made, in thirty minutes, twenty-eight round trips through *a*. During her absence in the nest, at the end of every ingoing journey, I changed the relative position of at least three centimeters of earth forming her path, and I gradually extended the displacements as far as from a^1 to a^5 , being careful to make the road level and quiet before her return. Not once did she hesitate or wander during all these journeys, although in the twenty-eight stirrings every millimeter of her trail had been displaced. Other ants were equally able to follow their trail over displaced portions of their path.

I also caused many marked ants to make trails over strips of wood covering the floor of the runs, and after the trails were established I turned the strips end for end, being careful to replace them so exactly that the continuity of the individual trail should not be broken. In no case did an ant give sign of having lost her trail. The advance of the ant over the reversed trail was unhesitating even when the reversed strip was so much as eight centimeters in length.

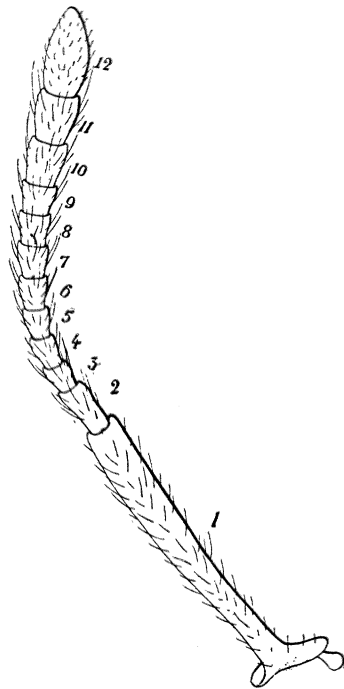
A layer of washed earth⁶ a millimeter or two in depth may be sprinkled upon the trail without destroying it, as does a thicker layer. The thin layer is doubtless pervious to the scent. The trail may also be moistened for a distance of several centimeters without destroying its continuity. But, as Bethe has pointed out, the ant can be thrown off its trail by wiping the floor on which the scent is laid, or by covering it with a strip of wood or of paper

⁶ Earth taken from any *Stenamma fulvum piceum* nest, well washed in running water and then dried.

from five to ten millimeters wide. The action of the ant when the scent is obscured proves that her trail is individual, and that it is under foot. She does not more readily pass the point of obscuration on account of it having been previously traversed by her comrades. Her action is the same whether she be the first to arrive at the newly-laid flooring or whether many ants have crossed it before her.

The power of perceiving the individual trail lies in the tenth segments of the antennæ. When deprived of this segment the ant is no longer able to find her way in with the pupæ, but wanders about helpless and bewildered. Ants deprived of nearly all of the eleventh and all of the twelfth segments continued to carry the pupæ through the runs of the maze, though with diminished physical vigor. The ant could pick up her scent so long as a tenth segment was intact, and no longer. For experiments in following the trail, I selected ants that had been previously distinguished by diligence in the carrying in of pupæ and later on set them to work with clipped antennæ.⁷

That *memory plays a part in the journeys as well as in other proceedings of the ant*, is shown by experiments made by me in gradually increasing the width of



LEFT ANTENNA OF *STENAMMA
FULVUM PICEUM*.

⁷ For removing the whole or any part of the antennæ of the ants used in the experiments described in this paper, the antennæ were clipped with sharp scissors, the wound was merged for five seconds in eighty per cent. alcohol to coagulate the blood; the ant was isolated upon a wet sponge in a Petri cell, without food, for a day, and was thereafter daily placed upon some acceptable food, such as moistened sponge cake, soft pie crust, or bread touched with honey. No insect food was given, and the cell was kept very clean. After fifteen days or longer about forty per cent. of the ants recov-

strips of paper or of wood-shavings laid over the trail. When the ant had well established her trail across the paper or shaving I could sometimes in her absence change it, replacing it exactly by a new one of the same color and material, and I have gradually increased its width from five millimeters to fifteen, or from one to three times her length, without causing the slightest distraction of the ant from her steady journeys to and fro over it.⁸ This proves that the ant does not smell her way at every point, and that familiarity with certain objects under her feet is gradually acquired. A dissimilar object, or an old object in a different place, never failed to distract the ant. The frequent placing of new objects upon her path, or repeated interruptions of her work, always caused her to change her route or to abandon her work.

Many ants, where records were kept, gained speed in the carrying in of pupæ, the number of journeys accomplished during an hour increasing always with experience of the runs, unless special hindrances occurred. If there be no greater stimulus in the greater amount of scent laid down, the gain in speed must arise from added familiarity with the road.

I occasioned one of my colonies to move from a Lubbock nest to its annex over a bridge eight inches long, once or twice a day during ten days, and the colony gradually reduced the time required for a complete change of location from over an hour to twenty minutes.

When an ant discovers a barrier across one of the runs in the maze, she does not more than two or three times follow her trail to the barrier, but altogether changes her route. In the change she does not merely cut off the loop in her own path, but she frequently takes a different direction.

ered from shock-effect and by their activities indicated their readiness for use in experiment. Before their recovery the ants were listless and abnormally irritable; and they attacked with self-destructive violence any moving thing that touched them. One antenna performs all the functions of a pair. In examining hundreds of ants, I found many with a single antenna, or with one antenna and the long proximal joint of the other, and these ants, including queens so maimed, were living normal lives. But I never found in its native nest any antennaless ant. The sense of taste is not lost with the antennæ. Ants kept without food for three days lapped honeyed cake with evident relish immediately after they were deprived of their antennæ. Their sensitivity to light, heat and humidity also remains unimpaired. No part of an antenna that had been clipped was regenerated during three subsequent months that I kept the clipped ants under my observation.

⁸ My best results were in using moistened brown blotting paper, care being taken that its edges across the path should be exactly even with the surface of the earth covering the floor.

The aptness of these ants to seek a new domicile whenever their nest is disturbed is perhaps correlated with the necessity of maintaining associations which give efficiency to a sensory memory.

Three worker-ants, without kindred, have lived in one of my Petri cells more than a year. They are perfectly at home in any new similar cell to which I transfer them. This surely indicates that they have become acquainted with their environment through other senses than that of smell.

Beside the scent whereby the ant lays her individual trail, every *Stenamma fulvum piceum* has an odor manifest in all parts of her animate body, and discerned by herself and by other ants through the eleventh segments of the antennæ.

It is improbable that the environment of the ants impart to them their odor. I found beside an old stone fence a colony rearing young under loose stones fifty yards apart. Workers taken from the discovered extremes of this colonial manor affiliated perfectly. From a space no larger than a quart-pot I took thirteen deälated queens in September, and eleven more the following June. Queens and workers of this colony met one another amicably after a full year of separation, although the one had spent that time in native soil, while the other had endured vicissitudes of travel, living in a glass house, feeding on human confections, and drinking water containing unlike mineral ingredients. I am also acquainted with two colonies whose swarming exits are but two yards apart, and these two colonies evince the intensest hostility to one another.

From among more than a hundred experiments that I have made, all yielding corroborative results in a study of the ant-odor, I give but a few examples:

The ant has an inherent odor. A callow five days old, that had been isolated nine days before emergence from the pupa-stage, was attacked and killed by the first ant it ever met, a callow of another colony.

Ants reared all the way from the larval stage without ant-nurses attract or repel other ants.

Ants were reared without ant-nurses, in sequestered groups, from pupæ of the same colony. When these ants were twenty days old the groups were united, and the ants at once affiliated.

Young ants, reared in an alien group, were returned to their

blood-relations. They were repeatedly dragged away from the nursery and were kept on probation until their personal odor was ascertained, and were within a day received into full association with their kindred.

A queen of colony D with four workers that she had reared from larvæ of the C colony, together reared three callows from pupæ of the E colony. When the callows were twenty days old, I put them in a Petri cell with adults of the E colony. The callows attacked the adults as with intent to kill, but they met with great toleration, and within a day all the inmates of the cell were living together in unity. In every case where callows were returned from among aliens to their own stock, the action of the adults bore a strange similitude to patient and forbearing discipline directed toward the reclamation of wayward offspring.

In a nest containing a queen and workers of colony C, I put a few young ants that had been reared in another section of the C colony from pupæ of the E colony. The young ants showed no fear of their new host, and were received with but slight sign of suspicion. They were treated as are alien ants smeared with the juices of kindred.⁹ But the superficial gloss did not long deceive, and at the end of the second day the young ants had all been killed and dismembered. Incorporation into one section of a colony never gave permanent safety in another section of the same colony that I had divided.

Workers of colony D alone reared four callows from pupæ of colony C. I segregated these callows and introduced to their cell four adults from another section of colony C. The adults immediately attacked the callows, indicating that they were overlaid with the odor of the workers that had fostered them; but the inherent odor of the callows was also influential, for none were killed, and the next day all the eight ants were clustered serenely in one group.

The odor is inherited through the queen. Five queens of the C colony, each sequestered with a few of her workers, reared from her own eggs several young ants. I am uncertain whether the five kings associated with these queens were of different colonies. The issue of any one queen would live in amity with the issue of

⁹ "A Study of an Ant," A. M. Fielde, *Proceedings of the Academy of Natural Sciences of Philadelphia*, September, 1901.

any other one of these queens, and all of the young ants would congregate around any one of the sister-queens.

Queens of the same colony have the same odor. Two queens, each having a similar mixed family made up of her own and a different stock, were interchanged with no disturbance of the domestic life in either nest.

Isolated queens of colony D reared each a few workers from pupæ of the C colony. The workers so reared would live amicably with any sister of the queen that reared them and also with one another.

A colony C queen and her issue reared two ants from pupæ of the E colony. When the two ants were a month old they were removed from the fostering family and were introduced into a cell containing a queen and adult workers of the C colony all deprived of the smell-sense. The young ants at once snuggled the queen and affiliated with the adults. They manifestly found in this sister-queen and her workers the exact odor to which they were accustomed.

I took two queens of the C colony and segregated each with pupæ of the E colony. After the pupæ had become ants fifteen days old, an exchange of queens caused no demonstration of surprise or of hostility.

The inherent odor of the queens and that of the workers in the same colony is of like quality, though the odor of a queen is probably stronger than that of a worker.

The behavior of kings in the nests proves them to be unable to distinguish between queens and large workers.

Workers removed from the C colony and segregated when eight days old received amicably, after nine months of separation, the two sister-queens in whose nests they had spent the first few days of active life. Unless their own odor was similar to that of these queens they must have had a personal memory of them. These workers rejected queens of another colony.

I isolated queens of the C colony and caused each to rear four callows from pupæ of the E colony. When the callows were sixteen days old I introduced into every queen's cell two colony C adults deprived of smell-sense. These adults were all received amiably by the callows, indicating that they had the same sort of odor as had the queen.

Ants hatched and reared to the age of twenty days with no association with any other ant received and affiliated with a queen of their lineage, though with some tentative nabbing.

Into a cell containing eight workers, of which equal numbers had been together reared from pupæ of two colonies, C and E, I introduced a C colony queen deprived of smell-sense. She was dragged away from the larvæ pile, but was not injured, and in six hours she was a fully accepted member of the mixed group.

Probably the odor discerned by the ants is something different from any discovered by human nostrils.

The odor preferred by the individual ant is determined by association, naturally during the first few days of its active life. Callows no more than three days old, having spent these days with a queen alone, with workers alone, or with both queen and workers, will thereafter withdraw from or fight any queen or worker belonging to any colony other than their own ancestral one, or those represented in their earliest nurses.

Pupæ of the E colony were isolated the last thirteen days of their pupa-stage, and their first meeting with any ant was when they were two days old, and was with a queen of the C colony. Within an hour the queen and the callows had perfectly affiliated. This queen had not been deprived of smell-sense; but during the long isolation of the pupæ, the E colony odor that earlier overlaid them had doubtless been dissipated, and they therefore presented to her nothing stronger than their own inherent odor as callows. Young callows from pupæ that have been isolated during the whole or nearly the whole pupa-period are safe in any colony. The immediate affiliation of these callows with an alien queen is the point to be here observed.

I sequestered pupæ from colony C and isolated the emerging unlicked callows. When these unnursed callows were two days old I put them into a Petri cell with a colony E queen and workers deprived of the smell-sense. The callows made no attack on the alien adults, but congregated beside the queen or workers as amiably as if all were of their own lineage. But callows likewise sequestered, isolated and reared to five days old with no association with other ants, could not be induced to affiliate with aliens. They established for themselves a criterion of correct odor, and withdrew from or seized any ant varying from their standard.

Queens and workers will usually live peaceably with any ant that they have reared from the pupa, and they may be caused to rear successive broods of unlike lineage, or to rear at one time a brood from eggs, larvæ or pupæ of diverse stock. But both queens and workers appear to be less at ease and to filiate less closely with such associates than with those of their own line, unless they greatly outnumber the introduced members of their group. If pupæ of alien stock are given to them in large numbers, shortly before the pupæ become callows, many of the callows are immediately killed. I segregated three groups, each consisting of a colony C queen and seven adult workers, and gave to each group eight pupæ from colony E. In two of these groups the pupæ all became callows within four days and all were killed. In the third group the pupæ were younger, none became active before the seventh day after being introduced, and five were permitted to live. These five callows had doubtless, during their longer residence in the group fostering them, been overlaid with the odor of the C colony, and therefore when they became active they bore an odor inoffensive to their adult companions. They were doubtless smeared with the odor of their hosts.

I have repeatedly seen a queen, with numerous workers of alien stock, flee from the group of ants that I had induced her to rear in her own nest. She had been unable to lick so many pupæ into her own likeness.

Ants remember, or are for some time positively chemotropic to, the odor to which they were earliest accustomed. An isolated queen of the D colony first reared four workers from larvæ of the C colony, and later on this mixed group reared three callows from pupæ of the E colony. When these callows were fifteen days old I removed them to the E colony, where they were happily domesticated five days. I then sequestered them in a Petri cell, and found that they instantly affiliated with either the D colony queen or the C colony workers that had earliest fostered them. They also affiliated with C colony adults deprived of the smell-sense.

Two queens of the C colony separately reared eight callows from pupæ of the E colony. When the callows were from eight to fifteen days old, I put the two queens into one Petri cell and the eight callows into another, and kept the C and E ants thus apart for thirty days. I then reunited the queens and the young ants and they again filiated, with no sign of distrust or aversion.

An artificially mixed group, now in my possession, was created partially by design and partially by incident, and it curiously illustrates my theme. As mentioned by Dr. W. M. Wheeler,¹⁰ *Stenamma fulvum piceum* sometimes feed their larvæ upon pieces of the pupæ of *Cremastogaster lineolata*. Desiring to know whether these ants would, when without larvæ, themselves devour the *Cremastogaster* pupæ, I gave a goodly number of such pupæ to each of several groups of *Stenammæ* living in Petri cells. In every group of *Stenammæ* some portion of the *Cremastogaster* pupæ was adopted and taken care of, at least during several days. In one group only, three of the *Cremastogaster*s were brought to the active stage, and continued to live with the *Stenammæ*s and to share their labor of rearing a single introduced male pupa. Probably these three *Cremastogaster* pupæ were so long in the care of the *Stenammæ*s that they were overlaid or smeared with the *Stenamma* odor before they became animate, and that their inherent odor was therefore obscured. Their own standard of congenial odor would, by earliest impression, be that of the *Stenamma* group. These *Stenammæ*s, which were of the C colony, had previously reared four workers from pupæ of the E colony, and I had removed these workers from their cell before the *Cremastogaster* pupæ therein had become active. The four workers had meantime been segregated in another cell. When the *Cremastogaster*s were about twelve days old, I returned the E *Stenammæ*s, after an absence of twenty days, to the C *Stenamma* cell. They were cordially received by, and at once filiated with, their foster C queen and workers, and they made no attack on the previously unknown *Cremastogaster*s. But the little *Cremastogaster*s attacked them frequently, until, in the course of a day or two, experience had shown them the futility of attempts on the life of newcomers so much stronger than themselves. *Cremastogaster lineolata* introduced from outside were killed under attacks from all the ants in this mixed group.

That *there is a relationship between the inherent odor of the ant and its color*, which gradually deepens with age, and that the odor of the queen is stronger than is that of her workers, is shown by the following experiment. I brought a colony from the woods, placed it in its native earth upon a Lubbock nest, and sequestered

¹⁰ "Habits of *Ponera* and *Stigmatomma*," *Biological Bulletin*, Vol. 2, No. 2.

many of its pupæ. I then segregated all callows that appeared on the same day among the pupæ, and in my experiment used none that had been nursed by any ant during the last three days of the pupa-stage, or that had ever met any ant other than those of her own age and lineage. When the callows were from sixteen to twenty days old, I introduced into a Petri cell containing several of the segregated callows single ants from among their blood-relations in the Lubbock nest. Ants of about their own age were always received with little attention and no nabbing; older workers with considerable attention and occasional nabbing; and very old workers or queens were attacked and pulled about by as many as three or four callows at once. The amount of excitement produced by the newcomer, and the number of attacks made upon her person, bore a direct ratio to the depth of her color. When an old worker had first been introduced and domiciled, the introduction of a second adult caused little excitement; but that of a queen called forth all the usual demonstrations of interest or distrust. If a queen was first introduced and domesticated, then the introduction of an old worker was an unimportant event. A second queen or a second adult was always received with lesser attention. I therefore think that the ants discriminate not only in regard to the quality of the odor presented, but also as to its intensity, and that the queen presents the ancestral odor in a more concentrated form than do her workers. None of these introduced ants attacked the callows, and all callows affiliated with the introduced ants within a day; but the fighting instinct of the callow is evidently aroused, not only by ant-odors to which it is unaccustomed, but by an intenser expression of its own inherent odor. If the older ants bore an adventitious odor through association with aliens reared in their nest, then the young ants would have borne the same odor and would have offered the same reason for attack.

With the purpose of ascertaining whether the odor of the ant was perceptible to other ants when deposited upon inanimate objects, I took a new unused maze and smeared the floor and walls of the *a* and the *n* runs with the juices of kindred queens and workers, and the *m* and *b* runs with the juices of aliens, leaving the *c* and *d* runs unsmeared. This smearing did not manifestly influence the ants in their choice of a route in carrying pupæ from *T* to *I*.

I then laid upon the floor of the *a* and *n* runs earth newly

taken from their own E nest, and upon the *m* and *b* runs earth newly taken from the nest of aliens, making the earth from the two nests to meet in the middle of the passages, 1, 2, 3, 4 Into *c-d* I put washed earth. Immediately after such distribution of the earth I put many ants from the E nest into the maze at *T* upon the pupæ pile, and recorded the number of journeys made through each run. Fully half the journeys were made upon the earth from the alien nest.

I then closed the *a* and the *n* runs and sent many ants of colony C over the *m* and *b* runs. While the trails were yet fresh, I removed the C ants and their nest, and gave the maze over to the E colony. The E ants in no wise avoided the *m* and *b* runs that had just been used by the C ants, but they traversed them as often as they traversed the runs through which no aliens had passed. Variations and repetitions of this experiment gave results always similar. I therefore think that the odor of the ant is discernible to other ants only when it is either perceived upon or is immediately disseminated from the living body of the ant. This view is sustained by the fact that alien pupæ placed in the nest just before they emerge from the pupa-stage are at first accepted by the ants, and are nevertheless often killed as soon as they cease to be inert.

I have found that the ant's power of perceiving this odor lies in the eleventh segments of her antennæ. The contact of these segments with any part of the body of another ant is followed by reflexes denoting either satisfaction or repugnance. When the ant is deprived of these segments by a cut across the tenth segment, she no longer discriminates between friend and foe. Deprived of these segments, marked ants of two or of five colonies lived peaceably together or fought one another with absolute impartiality. Forel discovered that ants of alien colonies ceased from hostile demonstration when deprived of the antennæ; but in my experiments this effect is as complete when no more than the two distal segments are removed. The removal of the twelfth segment alone is not effective, and as the segments telescope each into its proximal neighbor, the destruction of the tenth is necessary for the complete removal of the eleventh.

A healthy ant, with or without antennæ, will fight a dead ant, kindred or alien, if the dead ant be made to simulate an attack upon the live ant; and an ant will sometimes continue a battle

when all of its body except the head and one pair of legs has been clipped off. I have seen an ant, deprived of the smell-sense, continue through eighteen hours its grip upon an adversary's antenna. An antennaless ant will fight with energy and endurance, the difference between its battles and those of a whole ant being in that it fights indiscriminately the ants of its own and other colonies. In the complete ant the odor appears to modify, control or determine the fighting reflex.

In all cases of transfer from one kindred group to another there are evidences that the whole ants discern differences in the individuality of their companions whether queens or workers. Every newcomer is examined, sometimes from end to end, by touches of the antennæ; there is often much hesitating and tentative nabbing of an ant that is ultimately received into full fellowship, and two or three impetuous onsets often precede complete filiation.

In determining through their actions the affinities and repulsions of the ants, I have considered final relationships more important than first behavior.

The removal of the antennæ does not destroy the odor of the ants so maimed, for neither their enemies nor their kindred change on this account their usual behavior toward them. But the excision of these prominent organs reduces greatly their liability to seizure.

The commingled odors of all the ants in the nest constitutes what Bethe calls the Neststoff, or what I shall call the aura of the nest. It is diffused in air or ether from the animate occupants of the nest, and it is discerned by the ant through the twelfth, the distal, segments of her antennæ.

By this aura every ant recognizes its own abode and distinguishes it from the abode of other colonies. The aura of the nest may be superadded to, but does not extirpate, the individual scent nor the inherent body odor.

The creation of a new nest-aura is always possible through the gradual admixture of different odors produced by and disseminated from living ants reared from eggs, larvæ or pupæ of alien colonies.

Any ant bearing the preponderating odor is apt to gain easy admission to the nest. The countless variations observed in the treatment of newcomers are due to the infinitely variable proportions in the odors borne by the ants. If an ant permanently bears

an odor which is a component of the aura, she may be eventually accepted as an associate. If, in a group of ants reared in equal numbers from the pupæ of two colonies, C and E, I introduce an ant, deprived of smell-sense, from either the C or the E colony, the fearless newcomer is received with excitement and alarm and may be attacked with violence. But the attack is never fatal, and the blood-relative of half the group is eventually permitted to remain peacefully in the nest. When a whole ant from either C or E colony is introduced, the newcomer manifestly discerns an unfamiliar aura and either flees or else fights to a fatal end.

The sensitivity of the normal ant to the aura of an alien nest causes her to flee from it when escape is possible, and to endeavor to hide herself when she cannot escape. I have deprived many ants of the distal segments of the antennæ, and have found that on complete recovery from shock-effect their behavior was to be distinguished from that of normal ants by the absence of an exhibition of alarm when introduced into the nest of aliens. Such maimed ants do not flee, nor do they endeavor to hide, nor do they hesitate in close approach to a dense swarm of aliens. Their conduct when introduced into the nests of other colonies is strikingly different from that of the whole ant. Their action, whether in their own or an alien nest, evinces unconsciousness of the aura that determines the advance or retreat of the whole ant, or causes it, with uplifted and waving antennæ, to pursue an object that is beyond its reach. Callows reared from the third day of the pupa-stage with no association with other ants until the tenth day of active life, had then established their own aura, without the presence of a queen, and manifested alarm at the introduction of aliens.

If the subtile aura of the nest, imperceptible as it is to human nostrils, is diffused by a vibration in the body of the living ant which it envelops, the aura should be strongest where the greatest number of ants have longest lived. Its allurements in the air or ether may be what sometimes causes an ant to return to an old and empty habitation, and to carry back pupæ that have already been transported to a newly occupied nest.

The excitement occasioned by the intrusion of an alien among ants that are a few millimeters from the point at which the alien passes, indicates that the aura borne by the introduced ant extends at least a few millimeters from its body. The behavior of the

resident ants shows that the aura pervades the air or the ether, and gives intimation of the presence of the intruder without denoting her exact location.

The aura of an ant of the same colony appears often to determine the route of a companion not within touch of the antennæ, when burdens are being carried into the nest.

The distance to which the nest-aura is diffused may depend upon the number and quality of the living inmates.

Before an ant is five days old it has all its reflexes established, and appears to have sprung as from the head of Jove, full grown and completely accoutred, into active existence.

Callows that became such in the *T* corner of the maze straightway found a way into the nest, and commenced the carrying in of the inert young.

Callows less than five days old, that had never seen a queen, nor adults, nor earth, were transferred from their Petri cell to a handful of their ancestral soil, and they immediately built a nest with runs and recesses such as are made by experienced workers of their kind.

Prolonged captivity in a glass house does not diminish their ability to use earth in nest-making. I transferred to the earth on a Lubbock nest, when they were nine months old, some queenless ants that had always lived without earth in one of my artificial nests, and gave them a few larvæ and pupæ. Within ten hours they had made as perfect runs and recesses as any ever constructed by their species, and had disposed the young in the same manner as do their free congeners.

The unremitting attention habitually given by the workers to the young is hardly demanded by the necessities of the latter. I segregated eggs, larvæ and pupæ, and found that eggs untouched during several days bring forth normal larvæ; that with no attention from the ants the full-grown larva may successfully become a pupa; and that the whole pupa-stage may be safely passed with no more tending than such occasional changes of position as will prevent the growth of mould. *Penicillium crustaceum*¹¹ grows to ripeness, in either darkness or light, upon eggs, larvæ or pupæ, if left for a few days unattended in the humid atmosphere required by

¹¹ The moulds here mentioned were identified for me by Dr. George T. Moore, of Dartmouth College.

the ants, and its sprouting spores may be seen on their surfaces under a magnification of about five hundred diameters. If the spores are left undisturbed they cover the young with a delicate dense white coat that becomes sage-green with the ripening of the new spores. It appears probable that the ants find nutriment in the new mycelium of the mould, from which they relieve the young by licking them frequently and thoroughly. If the surfaces of the ant-children be a kitchen-garden spontaneously supplying the nurses with aliment, then these ants enjoy an economic independence surpassed only by that of an ideal creature that could lay eggs sufficient for its own nourishment.

This delicate mould does not grow upon the bodies of dead ants, but is there replaced by *Rhizopus nigricans*, with long and spreading hyphæ, and in this may lie the cause for the carrying off and casting away of all ants that die or are killed in the nest.

So long as the eighth and ninth segments of the antennæ are uninjured, the ant may continue to lift and care for the eggs, larvæ or pupæ, but after the removal of these segments she loses all interest in the young and performs no further work in the nursery. I proved this to be true in several colonies. In my colony B, which had been queenless during many months, the workers had been singularly devoted to the larvæ and pupæ from their own eggs,¹² and from among these ants I selected several that never failed to lift a larva when the cover of their Petri cell was taken away. Some of these assiduous nurses took all usual precaution for the safety of their young so long as the eighth segments of the antennæ were uninjured, but none lacking the eighth segment ever gave heed to nursery duties of any sort. From none of the other ants could I secure any attention to the young after the excision of the ninth segment.

Marked ants of two hostile colonies, when clipped across the tenth segment, associated freely and amiably with one another during several days in the care of pupæ belonging to one of the two colonies. A whole queen resident in the small nest appeared unable to tolerate the alien odor among the nurses, and often withdrew from the ever-alluring pupæ pile where they congregated. When the callows appeared, the queen aggressively took her place

¹² One of these worker's-egg-larvæ, separately reared, was one hundred and forty days in the larval stage.

among the young, and drove the alien nurses out from the nursery to the food-room, where they remained until I removed them. The queen's clipped workers continued to tend the young in the manner of whole ants.

On clipping the antennæ to the seventh segment, the middle of the segmented portion below the elbow, the ants lose all community of interest. In one of my large nests,¹³ used as a *hotel des invalides*, the ants never congregate, but stand separately and sometimes almost equidistant throughout the three rooms. The gregarious habit is probably a conjoint result of the reflexes from the five distal segments.

The instinct of following or huddling, common in young animals, is manifest in this ant during the first hours of its activities, when it keeps close to any accessible queen or worker.

The huddling instinct is apparently strong in its relation to ants of the same or lesser age. I isolated pupæ during the whole pupa-stage, thus freeing them, in their casting off of both the larval and the pupal integument, from all except the inherent odor, and I found that the callows huddled as soon as they were able to walk toward one another. The isolation of such callows for twelve days or longer did not diminish their tendency to huddle with ants of their own age or with younger ones of the same lineage. But from the twelfth to the twentieth day of isolation there was a marked diminution of the disposition to follow the queen and to huddle with adults. Dr. Edward Thorndike says¹⁴ that "if chicks do not have a chance to follow a hen in the first ten or twelve days they will not go near one if they have a chance." I have found no limit to the age at which a worker will follow a queen, but the attraction exercised by the queen is apparently due solely to association. When she or her kind has not been known during ant-infancy, her acquaintance is made with caution and reserve, if not with signs of distrust or dislike.

The ants appear to exhibit personal likings, aversions, affinities and antipathies. They seem to make and to keep individual acquaintances. They exhibit true social proclivities, and they manifest a possibility of surmounting race prejudices. Living mainly in darkness, they receive impressions through the antennæ

¹³ "Portable Ant-Nests," *Biological Bulletin*, Vol. 2, No. 2.

¹⁴ "The Human Nature Club," p. 26, *Chautauqua Press*, 1901.

rather than through the eyes, and they suggest the idea that the sense of smell may be as efficient as that of sight in appropriately connecting a creature with its environment.

I have observed that these ants, like the Termites, are able to carry water for domestic uses. They probably lap the water into the pouch above the lower lip and eject it at its destination. A hundred or two of ants that I brought in and left in a heap of dry earth upon a Lubbock nest, during the ensuing night took water from the surrounding moat, moistened a full pint of the earth, built therein a proper nest, and were busy depositing their larvæ in its recesses when I saw them on the following morning.